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EUGENE S. GAFFNEY AND GREG MCNAMARA

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□ *Reptilia, Chelonia, Meiolaniidae, Pleistocene, Australia.*

Eugene S. Gaffney, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York 10024, USA; Greg McNamara, Department of Geology, James Cook University, Townsville, Queensland 4811, Australia; 1 June, 1988.

The extinct meiolaniid turtles of the Southern Hemisphere are probably the most fascinating and enigmatic of the chelonians. Their appearance is bizarre, with cranial horns and frills and a tail club, and their relationships have been the subject of controversy for a century (see Gaffney, 1983, for literature review and previous work). Although many specimens have been found on Lord Howe Island, mainland Australia has yielded only one partial skull and fragmentary elements. The discovery of meiolaniid remains in northern Queensland extends the range of the group considerably (Table 1) and provides further evidence that at least two meiolaniid taxa existed on the mainland during the Pleistocene.

Abbreviations: AM — Australian Museum, Sydney; BMNH — British Museum (Natural History), London; MM — Mining Museum, Sydney; NMV — Museum of Victoria, Melbourne; ybp — years before present.

MATERIAL

The four *Meiolania* bones described below were deposited within the basal gravels of Unit A of the Wyandotte Formation, a Late Pleistocene sequence that outcrops along the banks of Wyandotte Creek, N Queensland (McNamara, this volume). Unit A is lowermost within the sequence and consists of two distinct lithofacies — a fossil-bearing granule gravel with clay matrix, and

a blue-grey clay from which fossils are unknown. On geomorphological grounds the base of Unit A cannot be older than a nearby basalt dated at 410,000 ybp, though here it is argued that the age is probably much less. Unit A basal sediments contain carbonised wood fragments beyond 14C range (45,000 ybp). The *Meiolania* specimens are therefore between 45,000 and 410,000 ybp. However, taking into account the time necessary to form an appropriate depositional centre, it is more likely that the specimens are between 45,000 and (approximately) 200,000 ybp. All four bones were found in an area designated as site 1 (McNamara, fig. 1, this volume) and occurred at roughly the same horizon, about 50 cm above the base of the Wyandotte Formation. Two horn cores (NMV P183195 — left; NMV P183196 — right) were in close association, lying oblique to the horizontal, suggesting that they settled in a scour, perhaps after having been washed free from the same individual. A third horn core (NMV P183197) and a caudal vertebra (NMV P183198) were deposited about 50 cm downstream and within about 3 m of each other. Both were lying within the plane of the beds and both show abrasion. The clay-dominated sequence of Unit A represents a vertical accretion facies, typical of a meander cut-off. It implies high runoff, frequent flooding and permanent water — a situation which allows *Meiolania* to occupy the niche traditionally associated with the mythical bunyips!

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BRIEF REVIEW OF THE MEIOLANIIDAE

DIAGNOSIS

Eucryptodiran turtles with squamosal and supraoccipital produced into large posterior and postero-lateral processes that extend clear of the skull roof; medial plate of pterygoid separated ventrally from basisphenoid to form the interpterygoid slit; broad squamosal-quadratojugal contact ventral to quadrate (from Gaffney, 1983).

INCLUDED TAXA

TABLE 1. Distribution of Meiolaniidae.

	Locality	Age
1. <i>Niolamia argentina</i>	Argentina	pre-Oligocene post-Jurassic
2. <i>Crossochelys corniger</i>	Argentina	Eocene
3. Undetermined meiolaniid	South Australia	middle Miocene
4. Undetermined meiolaniid	New South Wales	?Miocene
5. Undetermined meiolaniid	Queensland	Miocene
6. <i>Meiolania platyceps</i>	Lord Howe Island	Late Pleistocene
7. <i>Meiolania mackayi</i>	Walpole Island	Pleistocene
8. Undetermined meiolaniid	New Caledonia	Pleistocene
9. <i>Meiolania oweni</i>	Queensland	Pleistocene
10. <i>Meiolania</i> cf. <i>M. platyceps</i>	Queensland	Pleistocene

Niolamia argentina

A skull and tail ring described by Woodward (1888, 1901) from 'Cretaceous or Eocene' deposits in Argentina, differs from other meiolaniids in having a relatively large occipital frill (A, B, and C scale areas) and a small anterior cranial region. The B scale/horn area is wider, flatter, and relatively smaller than in other meiolaniids for which the area is known. The surface morphology of the skull is more or less well-known from Woodward's description but no sutures were described. A re-examination of the specimen is badly needed.

Crossochelys corniger

Simpson (1938) named a partial skull from the Eocene of Argentina and compared it with *Meiolania* and *Niolamia*. Although Simpson

regarded it as a distinct genus, Gaffney (1983) has suggested that it is a young individual of *Niolamia argentina*. The specimen is important in that it provides sutural and basicranial information. Even if it is distinct from *Niolamia*, these two taxa are closely related and may be compared as a unit with the Australasian meiolaniids.

Undetermined Tertiary meiolaniids from the Australian mainland

Fragmentary material from the Tertiary of South Australia and New South Wales has been identified by Gaffney (1981) as meiolaniid. The ages and localities of this material are documented in Gaffney's paper. Although the specimens reveal meiolaniids as important faunal elements in Australia to at least the middle Miocene, the absence (except as mentioned below) of skull material makes comparisons with the complete skulls of other meiolaniids difficult. One small B horn core (MM F13842) from the ?Miocene of Gulgong, NSW, shows close similarity to a small *Meiolania platyceps* B core figured by Gaffney (1983, fig. 25A; AM F18368). The Gulgong horn core is too small to show a marked degree of recurving but is more similar to *Meiolania platyceps* than to *Meiolania oweni*; it confirms the presence on the mainland of a taxon with recurved B horn.

Recent discovery by Dr Alex Ritchie (Australian Museum) of meiolaniid material from the Miocene Riversleigh deposits of western Queensland also extends the range of the group in the Tertiary.

Meiolania platyceps

The works of Anderson (1925, 1930) and Gaffney (1983, 1985) have made this taxon the best-known meiolaniid to date. Hundreds of specimens, including six skulls and three partial skeletons, are available for comparisons. The specimens were all found on Lord Howe Island, in calcarenites thought to be Late Pleistocene in age (see Gaffney, 1983, for review). The Lord Howe Island taxon exhibits a wide range of variation in many features of the skull and postcranium, but there is no evidence that more than one taxon is present, as the variation seems to be continuous (Gaffney, 1983).

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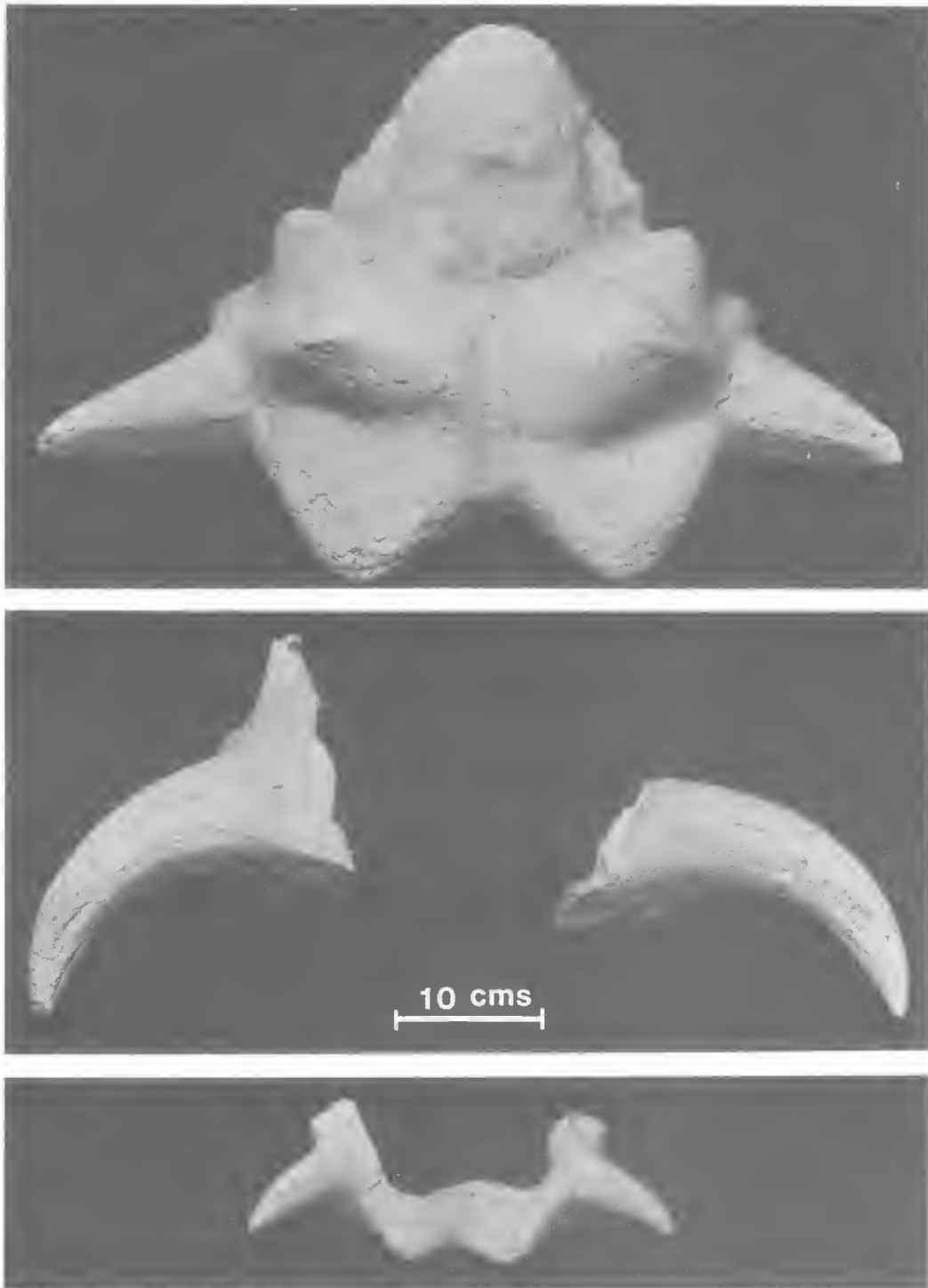


FIG. 1. Above — dorsal view of *Meiolania oweni*, BMNH R391, from Darling Downs, Queensland. Centre— dorsal view of NMV P183195 (left) and NMV P183196 (right) of *Meiolania* cf. *M. platyceps* from Wyandotte Station, Queensland. Below — dorsal view of AM F16866, *Meiolania platyceps* from Lord Howe Island, New South Wales. All photographs show casts at uniform scale

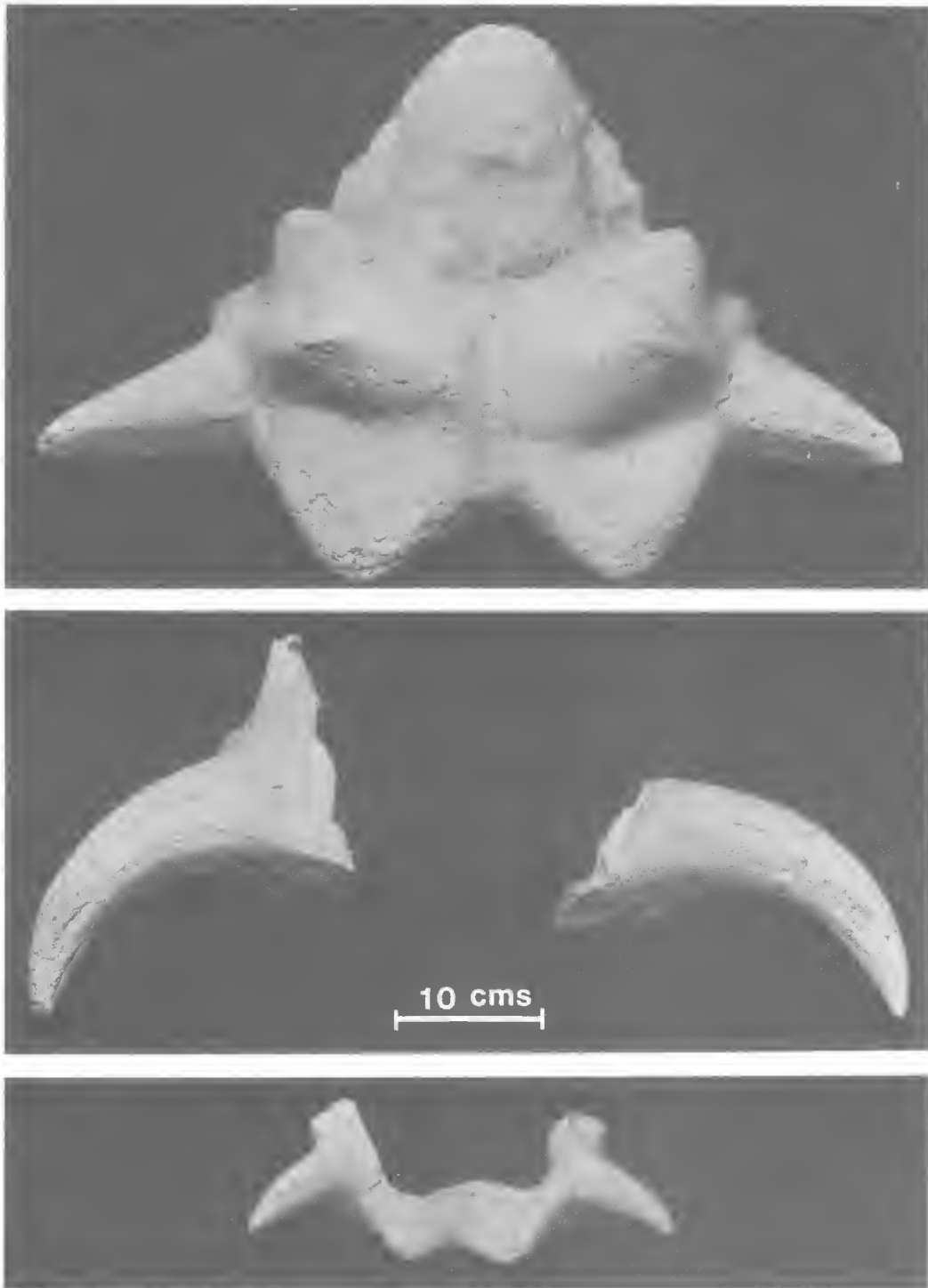


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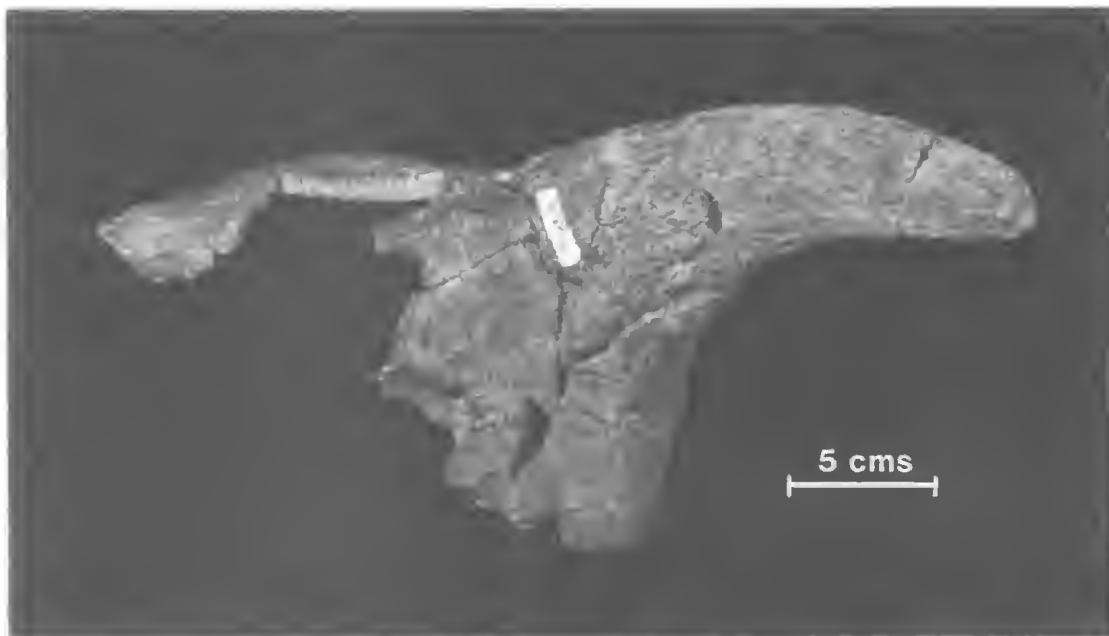


FIG. 2. *Meiolania* cf. *M. platyceps*, NMV P183197, Wyandotte Station, Queensland. Lateral view of left B horn core and fragments of skull roof. Anterior to left.

Meiolania mackayi and other New Caledonian occurrences

Anderson (1925) described some meiolaniid fragments from Walpole Island, including recurved horn cores similar to *Meiolania platyceps*, and assigned them to a new species, *M. mackayi*. The horn cores are consistently narrower than those of *M. platyceps* and seem to be from a smaller species (Gaffney, 1981). Subsequently Gaffney, Balouet and de Broin (1984) described meiolaniid cervicals from the main island of New Caledonia and a nearby island, extending the record of meiolaniids to three islands in the New Caledonian group (Walpole Island is about 100 miles SE of the main island).

Meiolania oweni

Owen (1881, 1882) described a large skull, tail club, and tail ring from the Pleistocene of King's Creek, on the Darling Downs of Queensland, and Woodward (1888) subsequently coined the name *Meiolania oweni* for this material. The skull (BMNH R391) differs conspicuously from *Meiolania platyceps* in having flat, laterally-directed B horns and a relatively large A horn scale area (see Gaffney, 1983, for more detailed cranial comparisons).

DESCRIPTION OF WYANDOTTE MEIOLANIID

Meiolania cf. *M. platyceps*

The Wyandotte meiolaniid material comprises three B horn cores and a caudal vertebra. Two of the horn cores, right and left, are very similar in size and shape and were found in close association. These cores, NMV P183195 (left) and NMV P183196 (right) are presumed to belong to a single animal and have been so restored in Fig. 1. The left core is more complete, consisting of a complete B horn area and much of the surrounding skull roof. The area of the C scale is preserved but the low boss of the C scale itself is broken off. Although sutures are not visible in any of the Wyandotte specimens, comparison with *Meiolania platyceps* from Lord Howe Island (figured in Gaffney, 1983) suggests that nearly all of the squamosal and some of the posterior part of the postorbital are present. Vento-laterally the dorsal margin of the cavum tympani is preserved and gives another landmark for comparison (see Fig. 2). Posteromedially the lateral one-third or more of the flat A horn area is preserved. The internal surface of the core is very similar to that figured by Anderson (1925, pl. 32, fig. 4), showing the squamosal formation of the

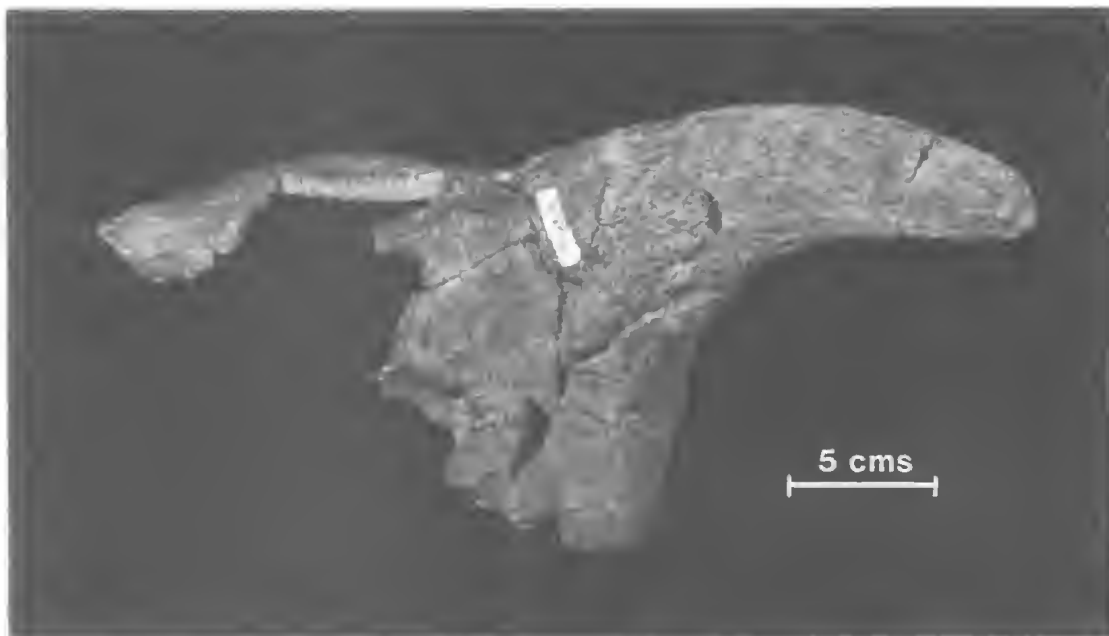


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antrum postoticum. The antrum is the postero-lateral corner of the cavum tympani and again provides a useful landmark. The right horn core also has a complete B horn and agrees closely with the left horn, but lacks more of the bone around its base. Both cores have the surface texture well preserved and show a coarse pattern of grooves and foramina usually associated with nutrient vessels, presumably for the horny sheath surrounding the core.

The third Wyandotte horn core, NMV P183197, is a specimen from the left side, with much more of the skull roof than in the other two examples. However, the B horn core is so badly weathered and eroded that none of the original bone surface remains.

The most striking feature of the three Wyandotte cores is the large B horn, which is the size and shape of a cow's horn. The curvature is particularly noticeable and more pronounced than in most of the Lord Howe Island horn cores. Nonetheless, the Wyandotte cores are very similar to the Lord Howe Island material (Table 2) and are nearly identical, except in size, to specimen AM F1209, figured both by Anderson (1925, plate 34) and by Gaffney (1983, fig. 24). As documented in Gaffney (1983), the Lord Howe *Meiolania platyceps* has B horns that vary a great deal in size and shape, though nearly every example exhibits some degree of recurving and is oval, not flattened, in cross section. *Meiolania oweni* has a B horn that is triangular with straight sides and is perceptibly flattened. The Wyandotte cores agree with the Lord Howe Island *Meiolania platyceps* in these features.

By contrast the Wyandotte material is similar to *Meiolania oweni* only in its size. The cores indicate an animal with a skull at least as large as *Meiolania oweni* and probably 10-20% larger. However, it is clear that the Wyandotte specimens are more similar morphologically to *Meiolania platyceps* than to *Meiolania oweni*.

A specimen in the Queensland Museum, brought to our attention by Ms Anne Burke and R.E. Molnar, supplies another possible locality for a recurved type of horn core. QM F2344 is the middle third or so of a B horn core, possibly the left. The core is very close in size and shape to the Wyandotte horn cores. It is clearly recurved and oval, rather than being straight and flat, as in *Meiolania oweni*. Unfortunately the label indicates nothing beyond 'old collection, no data'. The specimen was lodged with Darling Downs material, which it resembles very closely in preservation and matrix. It is extremely unlikely to have originated from Lord

TABLE 2. Comparison of horn cores.

<i>Meiolania platyceps</i> (Lord Howe Island)			
	Width	Height	Width/Height
AM F1209 (left)	4.7	9.6	.48
AM F1209 (right)	4.9	9.3	.52
AM F47544 (right)	4.5	7.5	.60
AM F16866 (left)	4.5	8.3	.54
AM F16866 (right)	4.5	8.4	.53
<i>Meiolania</i> cf. <i>M. platyceps</i> (Wyandotte)			
NMV P183195 (left)	8.5	20.5	.41
NMV P183196 (right)	8.5	21.0	.40
NMV P183197 (left)	9.0	18.5	.48

Howe Island, where the preservation is quite different, and it may well indicate that the 'recurved' *Meiolania* was more widely distributed on the Australian mainland.

A posterior caudal vertebra, NMV P183198, associated with the horn cores from Wyandotte, is nearly identical to caudals of *Meiolania platyceps* from Lord Howe Island, except in size. It bears particularly close resemblance to one example of the *M. platyceps* caudals illustrated by Gaffney (1985, fig. 15C; AM F18706). The haemal spine of NMV P183198, however, is more nearly vertical, as in AM F57984 (Gaffney, 1985, fig. 15B). In the restored tail of *Meiolania platyceps*, Gaffney (1985) suggested that AM F57984 was the fourth caudal while AM F18706 was the ninth or tenth; the total number of caudals in the restoration was conservatively estimated at ten. The caudal described here would appear to be placed posteriorly in the tail, judged on the centrum length and the low neural spine, but not at the end of the tail because the haemal arch is not sufficiently inclined.

The Wyandotte caudal lacks only a few areas: the distal portions of both transverse processes and the right prezygapophysis. There is nothing in the Australasian turtle fauna remotely similar to this caudal, but it appears morphologically primitive for Cryptodira (Gaffney, 1985) in retaining opisthocelous centrum articulations and well-developed haemal spines. Similar caudals are found in generalized cryptodires such as baenids and chelydrids in the North American fauna.

The only significant morphological difference between the Wyandotte caudal and *Meiolania platyceps* caudals is size — the centrum of the Wyandotte caudal being 11.2 cm long whereas AM F18715 is less than half as big (4.3 cm long).

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NMV P183197 (left)	9.0	18.5	.48

Howe Island, where the preservation is quite different, and it may well indicate that the 'recurved' *Meiolania* was more widely distributed on the Australian mainland.

A posterior caudal vertebra, NMV P183198, associated with the horn cores from Wyandotte, is nearly identical to caudals of *Meiolania platyceps* from Lord Howe Island, except in size. It bears particularly close resemblance to one example of the *M. platyceps* caudals illustrated by Gaffney (1985, fig. 15C; AM F18706). The haemal spine of NMV P183198, however, is more nearly vertical, as in AM F57984 (Gaffney, 1985, fig. 15B). In the restored tail of *Meiolania platyceps*, Gaffney (1985) suggested that AM F57984 was the fourth caudal while AM F18706 was the ninth or tenth; the total number of caudals in the restoration was conservatively estimated at ten. The caudal described here would appear to be placed posteriorly in the tail, judged on the centrum length and the low neural spine, but not at the end of the tail because the haemal arch is not sufficiently inclined.

The Wyandotte caudal lacks only a few areas: the distal portions of both transverse processes and the right prezygapophysis. There is nothing in the Australasian turtle fauna remotely similar to this caudal, but it appears morphologically primitive for Cryptodira (Gaffney, 1985) in retaining opisthocelous centrum articulations and well-developed haemal spines. Similar caudals are found in generalized cryptodires such as baenids and chelydrids in the North American fauna.

The only significant morphological difference between the Wyandotte caudal and *Meiolania platyceps* caudals is size — the centrum of the Wyandotte caudal being 11.2 cm long whereas AM F18715 is less than half as big (4.3 cm long).

CONCLUSIONS

Following a careful re-examination of the type and only known specimen of *Meiolania oweni*, we can substantiate the reconstruction of Owen (1881) and confirm the differences between it and *Meiolania platyceps*. Two questions remain. 1) Is *M. oweni* a taxon distinct from *M. platyceps*, or should it be included in that variable species? And 2) if these two are distinct, which horn core morphology is derived for the Meiolaniidae? More extensive comparisons of *M. platyceps* and *M. oweni* may be found in Gaffney (1983), who concluded that these were distinct taxa and should be recognized as different genera. *Meiolania platyceps* is a very variable species as presently interpreted, and recurved horn cores are known in New Caledonia and, possibly, the Tertiary of New South Wales; both of these occurrences may also represent different species, suggesting that the morphology is not limited to Lord Howe Island *Meiolania platyceps*. However, it is clear that *Meiolania oweni* is distinct from *M. platyceps* in more features than the shape of the horn cores (see Gaffney, 1983) and that *M. oweni* and *M. platyceps* are not one taxon.

If this conclusion is accepted, which set of characters for horn cores are derived with respect to the other? And can those characters be used to define a monophyletic group? The wide geographic distribution of recurved horn cores in the Australasian region might suggest that such a feature is more primitive, but comparison with *Niolamia-Crossochelys* suggests otherwise. The comparison of basicranial features by Gaffney (1983) showed that *Meiolania platyceps* could be interpreted as advanced with respect to the basicranial features of *Niolamia-Crossochelys*. If this hypothesis were extended to associated characters, then a weaker but reasonable hypothesis would be that the large frill and flat horns of *Niolamia-Crossochelys* are primitive for Meiolaniidae and that smaller rounded horns are derived. *Meiolania oweni* would be interpreted as advanced over *Niolamia* in this feature, but not so advanced as *Meiolania platyceps*, which has nearly lost the frill. In this interpretation the recurved horns would also be regarded as derived in relation to the flatter, straight cores of *Niolamia* and *Meiolania oweni*. From this argument, it might be concluded that all those species with the recurved B horn constitute a monophyletic group.

The Wyandotte locality is about 1400 km from the Darling Downs habitat of *Meiolania oweni* — which is about twice as far as the 700 km separating

the Darling Downs and Lord Howe Island. However, there is a lot of water in that 700 km, and so one might argue very reasonably that the Wyandotte meiolaniid should not be identified with the Lord Howe Island species. So, should the Wyandotte meiolaniid be named as a distinct species? At present it may be distinguished only on the basis of size and geographic provenance, and we do not consider that either criterion warrants the founding of a new taxon. Instead we prefer to express the existing uncertainty by identifying the Wyandotte meiolaniid as *Meiolania* cf. *M. platyceps*. The presence in the Pleistocene of Queensland of at least two species of gigantic meiolaniid is still interesting, whatever the nomenclature reflects.

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